

Millipedes as Aids for the Reconstruction of Glacial Refugia (Myriapoda: Diplopoda)

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ABSTRACT

This paper shows that we can discover Quaternary refugia by studying the present distribution of millipedes. Four preconditions are proposed that should be performed by a species used for the reconstruction of a refuge. It should have a low tendency of outspreading, it should be an endemic species, it should be easy to catch and its statements should be supported by other groups of organisms. Concerning two sites at the northern border of the Alps (in the vicinity of Basel/Switzerland and Salzburg/Austria) it is shown that some species of chordeumatids fulfill these conditions. The possibility of speciation after the Ice Age, the character of natural borders, the influence of extinction and men are discussed.

RÉSUMÉ

Utilisation des diplopodes dans la reconstitution des refuges glaciaires.

Ce travail montre qu'il est possible de découvrir des refuges quaternaires en étudiant la répartition actuelle des diplopodes. Quatre conditions préalables sont proposées, qu'une espèce doit remplir afin de pouvoir être utile à la reconstitution d'un refuge glaciaire. Elle doit présenter une faible tendance à la dispersion, être endémique, être facile à capturer et son statut doit être appuyé par d'autres groupes d'organismes. Il est montré que, dans deux sites de la bordure nord des Alpes (près de Bâle, en Suisse et près de Salzbourg, en Autriche), certaines espèces de chordeumatides réunissent ces conditions. La possibilité d'une spéciation post-glaciaire, les caractéristiques des frontières naturelles, l'influence des extinctions et celle de l'homme sont discutées.

INTRODUCTION

The idea of using the present distribution of animals for the reconstruction of glacial refugia has been born at the beginning of our century and is connected with the name of HOLDHAUS (1954), who investigated large parts of the eastern Alps. This research caused a dispute with JANETSCHEK (1956), the other one working on this subject. The main contradiction between them was the existence of inneralpine refugia (as JANETSCHEK stressed) against secondary immigration into those parts (HOLDHAUS' argumentation), however both principally agreed in the existence of glacial refugia in the Alps. HOLDHAUS (1954) mainly investigated beetles (especially wingless ground-beetles and weevils) while JANETSCHEK (1956) based his argumentation on a larger number of taxa. But even earlier the great german myriapodologist VERHOEFF (1917) recognized the importance of millipedes on this subject. He discovered the endemic species in the southern Black Forest and during many excursions in the Alps he

improved our knowledge on the distribution of these animals. A lot of his publications deal with the zoogeography of millipedes and he always tried to give explanations of their distribution, summarized in VERHOEFF (1938a).

MATERIAL AND METHODS

Beside the critical evaluation of the older (e.g. ATTEMS, 1949, BIGLER, 1913) and recent literature (e.g. SPELDA, 1991; PEDROLI-CHRISTEN, 1993), many collections have been made by the author since 1988 in southwestern Germany and in the northern Alps.

FAUNISTIC RESULTS

The following records have been unpublished up to now. Making localisation easier for subsequent workers the degrees of longitude and latitude are given for each locality. The sex of the specimens is represented by the scheme (males/females). Collectors are only listed if not identical with the author.

Abbreviations:

Xylvom = *Xylophageuma vomrathi* Verhoeff, 1911; Haanor = *Haasea norica* (Verhoeff, 1913); Hapocu = *Haplogona oculodistincta* (Verhoeff, 1893); Synace = *Syngonopodium aceris* Verhoeff, 1913; Pyrtit = *Pyrgocyphosoma titianum* (Verhoeff, 1910); Liscer = *Listrocheiritium cervinum* Verhoeff, 1925; Lisnor = *Listrocheiritium noricum* Verhoeff, 1913; Lissep = *Listrocheiritium septentrionale* Gulicka, 1965; Rhyale = *Rhymogona alemannica* (Verhoeff, 1910); Rhyser = *Rhymogona cervina* (Verhoeff, 1910); Rhyser = *Rhymogona serrata* (Bigler, 1912); Rhyver = *Rhymogona verhoeffi* (Bigler, 1913); Rhyweh = *Rhymogona wehrana* (Verhoeff, 1910); Rhy = *Rhymogona* sp.

A = Austria; CH = Switzerland; D = Germany.

CH: Aargau, 2 km ESE Sisseln (08°00'E, 47°33'N), 09.10.1991: Rhy (0/2); A: summit of the mountain Gaißberg (13°06'E, 47°48'N), 17.10.1991: Haanor (2/5); Lisnor (3/4); A: 1.5 km SW Scharfling at lake Mondsee (13°23'E, 47°47'N), 17.10.1991: Hapocu (3/3, *first record in the northern Alps*!); Synace (3/2); Lisnor (4/3); A: highway station "Tauernalm" (13°25'E, 47°15'N), 18.10.1991: Liscer (2/1); A: 3 km SSW Rossatz (15°30'E, 48°22'N), 21.10.1991: Lissep (3/1, *first record for Austria*); CH: Aargau, 1 km NW Sulz (08°05'E, 47°32'N), 27.10.1991: Rhy (0/6); CH: Aargau, 1.5 km SW Eiken (07°59'E, 47°31'N), 27.10.1991: Rhyser (2/1); D: 1 km N Hasel near Wehr (07°53'E, 47°39'N), 30.10.1991: Xylvom (4/1); Rhyweh (9/15); Pyrtit (3/1); D: 1.5 km SO Inzlingen (07°42'E, 47°34'N), 30.10.1991: Rhyser (10/8); D: N Maulburg (07°46'E, 47°39'N), 30.10.1991: Rhyale (3/1); D: 1 km S Schallsingen (07°39'E, 47°45'N), 30.10.1991: Rhy (0/6); D: 1 km ESE Wittlingen near Lörrach (07°40'E, 47°43'N), 30.10.1991: Rhy (0/1); D: 1 km NE Neckarhausen (08°39'E, 48°24'N), 01.11.1991: Rhy (0/1); D: 1 km E Marbach near Villingen (08°29'E, 48°01'N), 01.11.1991: Rhy (0/3); D: Obergießhof, 4.5 km S Hornberg (08°13'E, 48°10'N), 01.11.1991: Rhyver (1/2); D: Niedergieß, 3.5 km SSW Hornberg (08°12'E, 48°11'N), 01.11.1991: Xylvom (1/1); Rhyver (2/1); D: 1 km NW Hirschsprung, Höllental near Freiburg (08°01'E, 47°56'N), 01.11.1991: Pyrtit (1/0); D: 1 km SE Sulzburg (07°43'E, 47°50'N), 18.10.1992: Pyrtit (3/3); Rhy (0/2); D: E of Lörrach-Brombach (07°42'E, 47°38'N): Rhyser (2/4); D: quarry 1 km E Gerhausen (09°49'E, 48°23'N), pitfall trap, 17.09.-01.10.1992, leg. J. BÖHMER: Rhyser (1/0); D: Scheibenfelsen SE Häusern (08°10'E, 47°44'N), pitfall trap, 12.1988.-05.1989, leg. R. MOLEND: Rhyweh (1/0); D: Prag 6 km SSE Todtnau (07°57'E, 47°46'N), pitfall trap, 10.1991, leg. R. MOLEND: Pyrtit (5/8); D: S Badenweiler (07°40'E, 47°47'N), 07.10.1986, leg. A. PEDROLI-CHRISTEN: Pyrtit (0/1); D: S Hierbach (08°05'E, 47°40'N), 08.10.1986, leg. A. PEDROLI-CHRISTEN: Pyrtit (0/1); D: 1 km SW Altglashütten (08°05'E, 47°51'N), 30.09.1990, leg. A. PEDROLI-CHRISTEN: Pyrtit (1/0).

DISCUSSION AND FURTHER RESULTS

A. Conditions for the use of a species as an aid for the reconstruction of glacial refugia

The use of the present distribution of organisms for the reconstruction of glacial refugia is based on the assumption that it mainly is a consequence of the depauperation during the Ice Age. The main argument for this is, that neither petrophilous (meaning restricted to rocky areas) nor endemic animals occur in Scandinavia (HOLDHAUS, 1954; VERHOEFF, 1938a), although we have similar climatic conditions than in the Alps. As Scandinavia was totally covered with an ice-shield during the glaciated periods (NORDAL, 1987) we have a very good explanation for this fact.

To increase the suitability of the used organisms and consequently the validity of their distribution for our purpose, the following conditions should be performed:

A. 1. Low tendency of spreading out

This is of course very important, because there might have been many species that have survived at the refugia. But if they largely spread out after the climate had changed to better conditions their vestiges got lost. Only the few species, that did stay nearby their former refugia, will show us where they have been situated. In some cases the present distribution indicates a north-alpine persistence (e.g. in the beetle *Trechus glacialis*) but it cannot be proved where this species has survived and whether it had a monocentric or polycentric refuge. Automatically this means the more restricted a species is, the better it is suitable for the reconstruction of glacial refugia.

A. 2. Speciation

Endemic species will provide a stronger argument for a refuge than isolated populations of a wider distributed species (but also see below under C. 3.). Without knowing of possible vectors, we simply cannot decide whether there had been a polycentric refuge including several nunataks or massifs de refuge or if the species has obtained parts of its present distribution in more recent times.

Of course we have to ask the question why speciation should take place in the small, isolated populations on their refugia. Referring to this, the theory of "sexual selection by female choice" (EBERHARD, 1985), is of importance. Using its arguments we might suppose that in a small area with a low amount of natural resources (food, hiding-places, etc.) there must be an intensive struggle between the males about the females. These favour males on the base of their genitalia, so that we have a strong selective pressure to surpass the competition. As the direction of this evolutionary process is of random, different populations will go different ways. The smaller a population is, the faster this process will go on.

At smaller refugial areas or at the border of larger ones, suitable places for the survival will be intermitted by hostile areas, e.g. ice streams. As a result of this partition we will probably find a complex of sibling species or subspecies at such places that furnish proof for this.

A. 3. Easy to catch

This condition is of practical value for the researcher and certainly depends on his experience. But there are some species that live at inaccessible places or occur in so low numbers that they will be found only by chance. We know of many species that have been described as being endemic and have later been found elsewhere. Good examples are subterranean species, especially the phreatic species that live in small crevices deep inside the rocks, where equal climatic conditions occur. Most of them have been described as cave species, simply because caves are the only places where men and phreatic species can meet.

A. 4. Confirmation by other organisms

If we do not assume that the outlasting was only a special case in one species or genus, we might expect that endemism may also occur at other groups. This means, the more endemic species from different groups (millipedes, beetles, earthworms, etc.) occur, the better a possible refuge is verified. On the other hand there may occur isolated populations of non-endemic species at this places too. Although we cannot exclude a secondary immigration (even with human influence, see below) they may support our conclusions.

B. Biogeographic reference for the refugia near Basel and Salzburg

B. 1. The refugia in general

Many of the classical localities of former investigators have been visited and in most cases it was possible to confirm the occurrence. It has been proved, that the genera *Haasea*, *Xylophageuma*, *Syngonopodium*, *Pyrrocaphosoma*, *Rhymogona* and *Listrocheiritium* perform the condition of being relatively easy to find. It is most important to choose the right time. At the middle to late October they will be quite common under bark and dead wood. Nevertheless there are differences between the genera: *Rhymogona* and *Pyrrocaphosoma* will be found quite regularly in October, with no or only minute dependence from the weather. In spite of BIGLER's (1913) opinion *P. titianum* is quite common, but strongly related to high humidity, so that it is mostly found near springs and small brooks. *Xylophageuma vomrathi* is much more difficult to catch, possibly contrary to its sibling species *X. zschokkei*, that was found quite common by PEDROLI-CHRISTEN and myself during our excursions in the Vosges Mountains and the Jura. But although we both collected *Pyrrocaphosoma* and *Rhymogona* quite regularly, PEDROLI-CHRISTEN has never found *X. vomrathi*. Its occurrence seems to depend on cold weather with temperatures just above the freezing-point.

Other species, like the possibly phreatic ones *Alpityphlus seewaldi* (only one record known, STRASSER, 1967), *Polydesmus rothi* and *P. xanthocrepis* have very seldom been collected and seem to be not suitable for a survey. Nevertheless, as long as we have no contradictions for their endemism, we may use them as additional arguments for the refugia.

At the investigated sites the endemic species have been found sympatric and often syntopic under the same bark, in community with a rich fauna of other millipedes. During the investigations, at two places (Hasel, Scharfling) the maximal amount of endemic Chordeumatida has been found syntopic. This supports the assumption of a glacial refuge and contradicts the conception that the endemism results from competition with superior species.

Both refugia contain limestone areas. This might be of general importance for glacial refugia, as calcareous areas mean warmer soil and the crevices provide places with moderate, although cold climatic conditions, that may render a retreat during hard times.

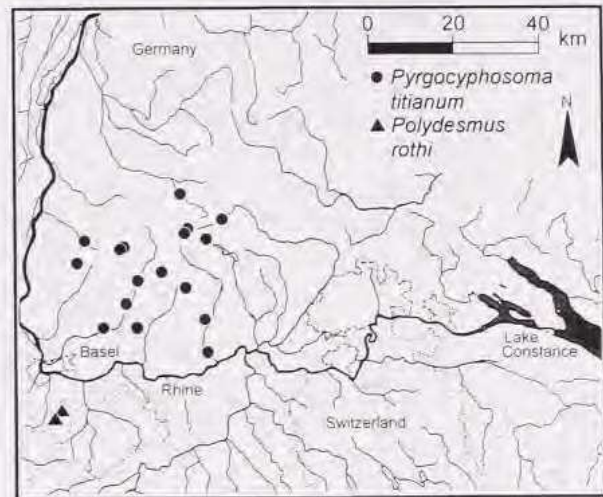
B. 2. The "Basel-refuge"

When comparing the maps (Figs 1-3) *P. titianum* shows the most closed distribution of its records, so that it is regarded as the most suitable species for reconstructing the "Basel-refugium". The three endemic *Rhymogona*-species indicate a partition to at least three different sites. A possibly similar species-complex occurs in the snail genus *Bythiospeum*.

Another endemic animal in the southern Black Forest is the earthworm *Lumbricus badensis*. Its distribution (KOBEL-LAMPARSKI & LAMPARSKI, 1989) is much the same as in *P. titianum*. Other endemisms in this region are known from snails (*Bythinella badensis*, *Bythiospeum sterkianum*, SCHMID, 1979; SCHMID, 1989). In the snail genus *Trichia* 4 endemic species are known from northern Switzerland and adjacent Germany (*T. caelata*, *T. clandestina*, *T. graminicola*, *T. biconica*, KERNEY *et. al.*, 1983), with *T. caelata* having a similar distribution as *Polydesmus rothi* (Fig. 1). In the caves of the northern Jura the endemic cave-beetle *Royerella villardi matheyi* occurs. Somewhat more southward in the Jura we will find other cave animals like *Trichaphaenops sollaudi* (Coleoptera), *Trichonisoides pulchellus* (Isopoda),

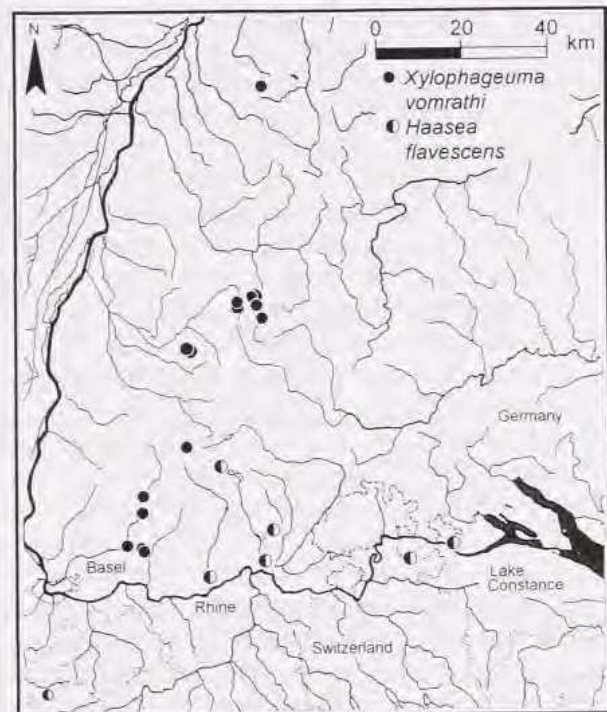
Archiboreoiulus sollaudi and *Boreoiulus simplex* (both Diplopoda). As a support from wider distributed species we have isolated populations of subalpine plants like *Primula auricula* (MEUSEL *et al.*, 1965-92) and beetles like *Nebria gyllenhali* (missing in the Vosges Mountains) that occur in the Black Forest.

FIG. 1. — Distribution of *Pyrgocyphosoma titianum* and *Polydesmus rothi* in southwestern Germany and adjacent Switzerland.



The lack of the endemic Black-Forest-species, as well as related species in Switzerland (PEDROLI-CHRISTEN, 1993), at the alpine level contradicts a nunatak-refuge and supports a massif de refuge at lower altitudes. When we decrease the formerly glaciated areas (HANTKE, 1978-1983), the calcareous mountains at the southern border of the Black Forest remain as most probable refuge. This might be supported by the sympatric occurrence of members of all three endemic genera and the junction of the ranges of the three endemic *Rhymogona*-species. In agreement with a map provided by HANTKE (1978-1983) we are even able to attach the ice-free parts of the southern Black Forest as refugia to each of the endemic *Rhymogona*-species.

FIG. 2. — Distribution of *Xylophageuma vomrathi* and *Haasea flavescens* in southwestern Germany and adjacent Switzerland.



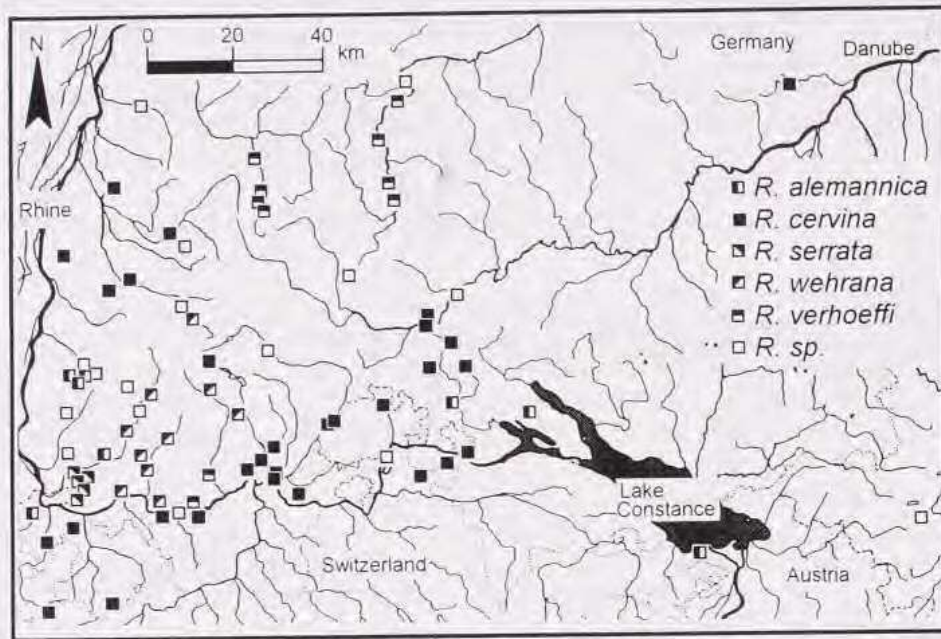


FIG. 3. — Distribution of *Rhymogona* species in southwestern Germany and adjacent Switzerland.

B. 3. The “Salzburg-refuge”

The “Salzburg-refuge” can be delimited by the occurrence of *Syngonopodium aceris*, *Haasea norica* and *Listrocheiritium noricum* (Figs 4-6). At present time we still have gaps in the knowledge of the millipede fauna in northern Austria, so that not too many conclusions about the exact extension of the refuge should be drawn. The results are in accordance with HOLDHAUS (1954), and we can add the beetles *Trechus wagneri* and *Otiorhynchus schaubergeri* as further endemisms of this region. Very interesting is the occurrence of the also endemic cave beetle *Trichaphaenops angulipennis* in the Dachstein-mountains, an area regarded as being glaciated during the Würm. But as phreatic/cave species are difficult to record this species might have survived at the unglaciated sites nearby. Its distribution resembles *Syngonopodium cornutum*. As the eastern Alps have only been slightly glaciated (HOLDHAUS, 1954), the number of endemic species increases eastward, so that we might assume a series of refugia along the northern Alps from Salzburg on. This is supported by the distribution of the genus *Listrocheiritium*, showing a sequence of species there. The isolated record of *L. nubium* in the mountains of the “Totes Gebirge” is very strange and may refer to *L. noricum* as a possible misidentification. *L. cervinum* has a wider distribution inside the Alps, and the new record (“Tauernalm”) fills the gap between the mountains of Hochstaufen, Grimming and Großglockner. *Listrocheiritium*-species show a large vertical distribution, reaching the alpine level and have possibly survived on both, nunataks and massifs de refuge. The Austrian record of *L. septentrionale* (Rossatz) is identical with “Buchental bei Spitz” given by ATTEMS (1949) as locality for the never described *L. nibelungiacum*. Examination of topotypic specimen and ATTEMS’ types proved their identity, although *L. septentrionale* has been described from a site more than 80 km northerly. This may show, that in contrast to VERHOEFF’S (1917) opinion large rivers like the Danube provide no hindrance for Chordeumatida. As most parts of northern

Austria are myriapodological badly investigated this species might be well distributed in the intermediate area.

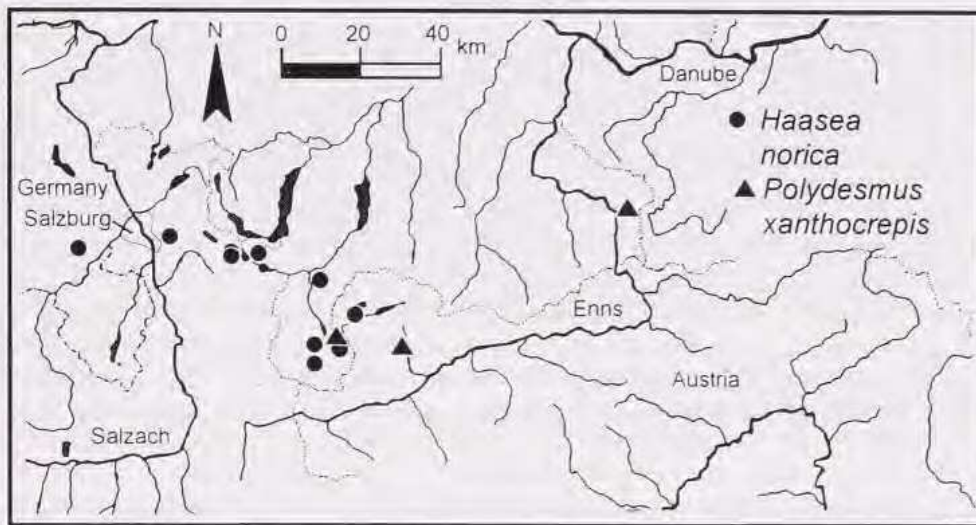


FIG. 4. — Distribution of *Haasea norica* and *Polydesmus xanthocrepis* in the northeastern Alps.

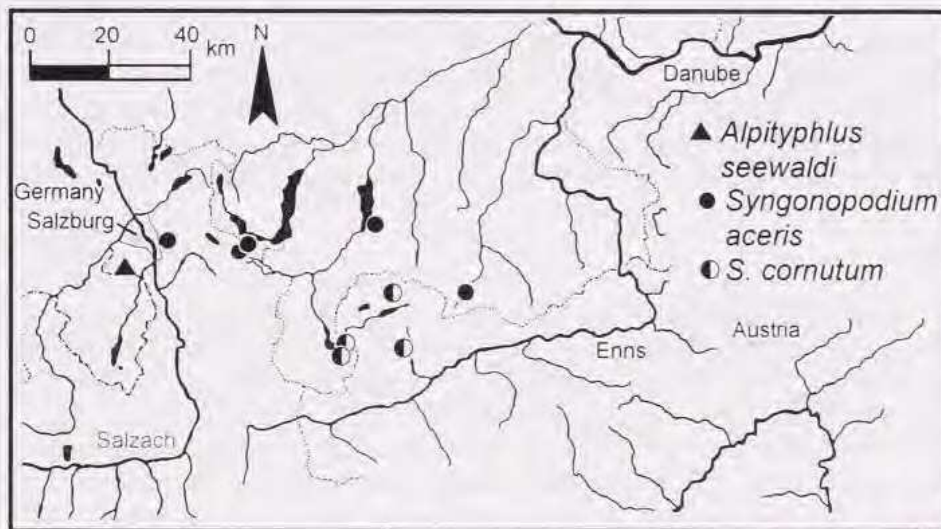


FIG. 5. — Distribution of *Alpityphlus seewaldi* and *Syngonopodium* species in the northeastern Alps.

Isolated populations of wider distributed species, that support the “Salzburg-refuge” are found in many snails e.g. *Acicula gracilis* and *Renea veneta* (KERNEY *et al.*, 1983). In respect of this, the isolated occurrence of the chordeumatid *Haplogona oculodistincta* at Scharfling is very interesting, as it could belong to a relict population. As this site provides a rich, pretentious

millipede fauna, synanthropism might be excluded. The species is distributed in the southeastern Alps up to Vienna and adjacent Balkan Peninsula.

C. Discussion of problems and counter-arguments

C. 1. Speciation after the Ice Age

Someone may argue, that the endemic species have been developed after the time of glaciation. An argument for this is the occurrence of endemic plants like the *Papaver radicatum* complex, on which a discussion for ice-free refugia in Scandinavia was based on. NORDAL (1987) showed, that we can explain the endemism by postglacial immigration and subsequent speciation. This is certainly in larger accordance with the geological results there. The question is, can we transfer this to animals? The arguments against are, that we have no similar endemisms of animals in Scandinavia, and that plant "speciation" can occur extremely rapid by a single mutation with distinct phenotypic effect. As the presence of a mate is not absolutely necessary (self fertilisation) a single specimen can be the ancestor of a whole changed population beside a refuge. Animals, if not parthenogenetic, are liable to bisexual propagation, that will suppress extraordinary mutations if they are not advantageous. In times of spreading, when there are less meetings of males and females sexual selection would be less effective (EBERHARD, 1985).

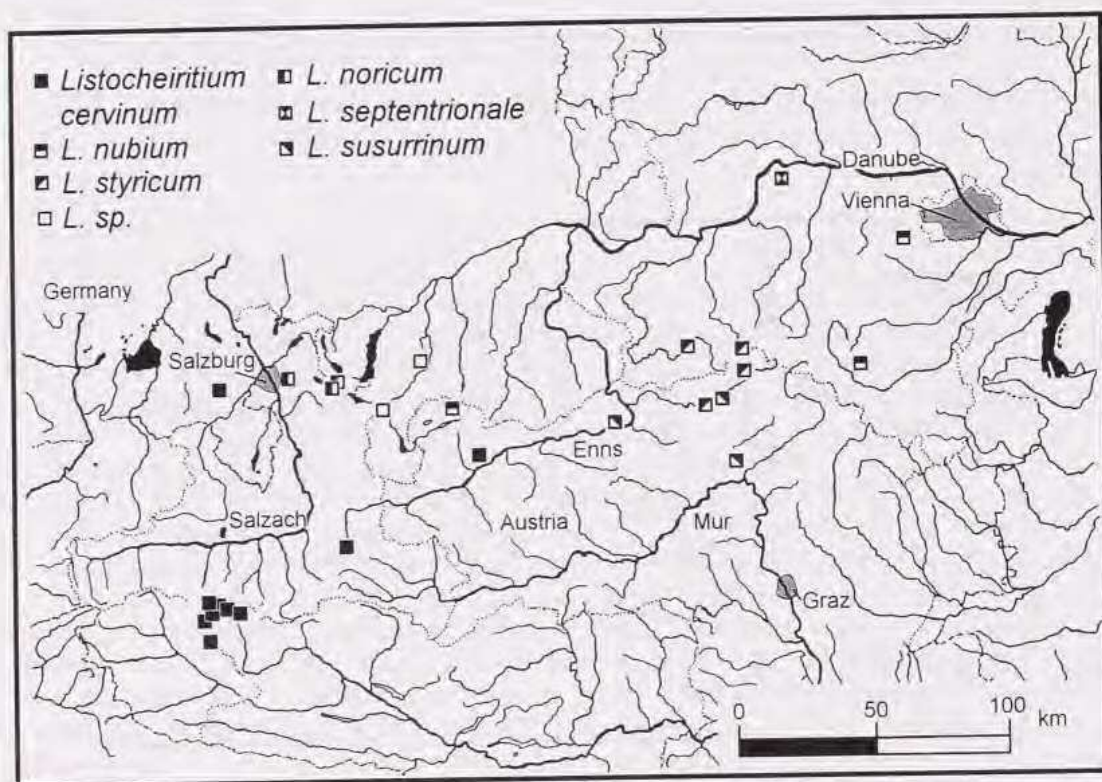


FIG. 6. — Distribution of *Listrocheiridium* species in the northeastern Alps.

C. 2. The character of natural borders

VERHOEFF (1917) was the first who discovered the importance of rivers as distributional borders. An argument against them as absolute borders for millipedes might be the occurrence of species with generally small ranges on both sides of the Danube (*Listrocheiridium septentrionale*,

Haploporatia eremita, *Leptoiulus marcomannius*) and the Rhine (*Rhymogona cervina*, *R. alemannica*, *Orthochordeumella fulva*, *Polydesmus helveticus*, "Helvetischer Rheintaldurchbruch" of VERHOEFF, 1917).

With respect to EBERHARD's (1985) hypotheses I will propose another explanation. If two species have been separated only by sexual selection they still use the same ecological niche. As we know that two species cannot occupy the same niche at the same time, they must occur allopatric or parapatric (vicariance). If we assume that their selective fitness is quite equal, the native species is in favour against the invasive. As a result we will have relative stable borders at places that will not be crossed so often like rivers and mountain ridges. This explains the complex distribution of the genus *Rhymogona* in southwestern Germany much better, as the distribution follows small rivers and brooks with species often changing between parallel ones and - on the other hand - changing between larger rivers like the Rhine and the lower course of the Wiese. The parapatric distribution of the related species *Xylophageuma vomrathi* and *Haasea flavescens* (Fig. 2) might be another case of parapatry by ecological competition.

C. 3. "Natural" extinction

Endemism can not only be explained by speciation e.g. during the ice-age, including reduction of the areal and - up to now - only a minute reimmigration, but also by reduction of the distribution caused by other (ecological) effects like competitors, enemies and diseases. The occurrence of such palaeoendemisms may simulate a glacial refuge, but normally in this case we will have more than one isolated population of the same species (meaning places where the hostile conditions are not effective) or they occur on special places, where other species cannot survive (displacement to extreme sites). In spite of this, the places where the endemic millipedes occur contain a very rich fauna so that we may regard displacement as less probable.

C. 4. Human influences

There might be the possibility that a species is delimited to a small area that cannot be left naturally. But if transported by men, perhaps with the earth surrounding a plant, it may arrive a place where spreading means no problem. This has been followed quite profound in North America by the invasion of European species. Perhaps this is also a good explanation for the colonization of the British Island by millipedes, as they might have been companions of early settlers. On the other hand devastation by men took part in many of the areas populated by him, e.g. by cutting down the forest. So we might also think of the change of areals by men in recent and former days.

CONCLUSIONS

Comparison of the refugia presented here with the map of true cave-animals given by HOLDHAUS (1954) shows, that the northernmost parts of their distribution cover with them. Also a map provided by JANETSCHEK (1956) shows our refugia being included, but as demonstrated here, they are more ensured and obviously of larger importance than most of the other north-alpine "refugia" shown by him. So there is much evidence, that the southern part of the Black Forest and the mountains of the Salzkammergut are the northernmost places where a pretentious fauna have survived at least the last glaciation (Würm) in middle Europe (excluding the Carpathians). Although there might have been no larger trees, there is much evidence that *Salix*-species have survived the last cold stage north of the Alps (BENNET *et al.*, 1991). Their litter might have served as food for the persistent diplopods.

An interesting aspect has been pointed out on forest trees by BENNET *et al.* (1991), saying that remainig tree populations at mid-altitude sites in the mountainous areas of southern Europe are most important for the long-term survival of species, as they cannot follow the rapid climatic changes. As a result, the refugia are important at all times, both cold and warm stages. This might also be true for animals with a low tendency of spreading out and may explain the "petrophilism" just because of the fact that mountains show closed sites with different climatic

conditions, that allow changes to suitable biotopes, so that a long-distance travelling to such places is not necessary in cases of global climatic changes.

As no one can travel through time and test hypotheses concerning the past, we have to use the "principle of parsimony", that is also used in the discussion of phylogenetic pathways, meaning that we favour hypotheses that need less additional assumptions than others. The present distribution of organisms seems to be an important argument in cases where we have no pollen evidence or macrofossils. With the exception of three phreatic/cave species (*Alpityphlus seewaldi*, *Polydesmus xanthocrepis* and *P. rothi*) the endemic millipedes all belong to the Chordeumatida. This shows, that the members of this order are the most important indicators for our purpose.

Up to now, no other group is known, showing so much endemism in the European mountains as the millipedes (VERHOEFF, 1938b) and especially the chordeumatids. These species - "Glazialresistente" of VERHOEFF (1917) - must be considered as being preglacial or at least interglacial relicts.

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